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Invited Review Article

Wheat genome phylogeny and improvement

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Abstract

Poaceae (formerly known as Gramineae) is often considered to be the most important of all plant families to human economies. From evolutionary point of view, wheat is a young polyploid and its genetic configuration is a classical example of cereals phylogenic relationship. The genetic diversity of the elite germplasm have been used by plant breeders for numerous reasons such as germplasm management, genetic relationships, parent selection, and protection. Hence, the knowledge of genetic diversity and relationship among a set of germplasm is of great importance in present scenario for crop improvement and genetic security of food grains. Similarity of wheat genome with rice and maize pave a way to develop more improved verities' of wheat. Many good stress-tolerant wheat verities have developed in the light of phylogenic study of these species. The focus of this review paper is to highlight phylogenic relation of elite wheat genome as well as laconically development of the new stress tolerant wheat varieties.

Keywords: abiotic stress; biotic stress; phylogenic relation; selectable marker; transgenic wheat; wheat genome
Abbreviations: BAC, bacterial artificial chromosomes; BLAST, Basic Local Alignment Search Tool; ESTs, expressed sequence tags; FHB, *Fusarium* Head Blight; GRRs, gene-rich regions; *GUS*, β-glucuronidase; *LEA*, late embryogenesis proteins; PAC, P1-derived artificial chromosome; QTLs, quantitative trait loci

Introduction

The grasses, members of the monocot family Poaceae representing 10,000 species belonging to 651 genera (Clayton and Renvoize, 1986) are distributed worldwide. Wheat is an important member of the family Poaceae which includes major cereal crops of the world such as (*Oryza sativa* L.), maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), sorghum (*Sorghum vulgare* L.), barley (*Hordeum vulgare* L.), rye (*Secale cereale* L.) and several others. It is a grass, originally from the Fertile Crescent region of the Near East, but now cultivated worldwide. In 2007 world production of wheat was 607 million tons, making it the third most-produced cereal after maize (784 million tons) and rice (651 million tons). Among the food crops, wheat is one of the most abundant sources of energy and proteins for the world population. Wheat genetics is more complicated than that of most other domesticated species: it is an allopolyploid, containing three different ancestral genomes (designated A, B and D), each of which contains seven pairs of homologous chromosome (Kumar and Singh, 2010; Hussain et al., 2010). The number of chromosomes in the diploid genome (2*n*) is therefore 42; this number is also referred to as 6x, as each of the six ancestral genomes has seven chromosomes. Some wheat species are diploid (*T. monococcum*), with two sets of chromosomes, but many are stable polyploids, with four sets of chromosomes (tetraploid e.g. emmer and durum wheat) or six (hexaploid). Wheat is a staple food and main source of carbohydrate hence researches are interested in increasing yield of wheat through biotechnology techniques. New biotechnology techniques combat the drawbacks of conventional breeding techniques which are based on processes of crossing, back crossing and selection, proved to be time consuming and, therefore, could hardly keep pace with the rapid co-evolution of pathogenic micro-organisms and pests (Powell and Langridge, 2004). In concert with traditional plant breeding practices, biotechnology is contributing towards the development of novel methods to genetically alter and control plant development, plant performance and plant products. The use of DNA sequence-based comparative genomics for evolutionary studies and for transferring information from model species to crop species has revolutionized molecular genetics and crop improvement strategies. Most of the agriculture biotechnology techniques are based on genetic engineering in which genome of plant is manipulated to increase the grain yield and to minimize crop loss due to unfavorable environmental conditions, and attack by various pests and pathogens (Patniak and Khurana, 2001).

Wheat genome

Gene numbers in different plant species are not expected to vary greatly. In rice, the latest estimate places the number of genes around 32,000 (The Rice Annotation Project, 2006). In maize, an ancient tetraploid, gene numbers are expected to be in the range of 37,000 to 63,000 (Chen et al., 1998). Studies on the genome organization of wheat suggested that more than 85% of the wheat genes are present in less than 10% of the chromosomal regions (Deepak and Gill, 2004).

A conservative estimate based on the annotation of 11.1 Mb of sequence from randomly selected BAC clones, and taking into account the fact that gene numbers varied by as

much as 32% when the same sequence was annotated by different people, is that the wheat genome contains between 164,000 and 334,000 protein-encoding genes, including pseudogenes (Devos et al., 1994). physically mapping have found that wheat contain 3025 loci including 252 phenotypically characterized genes and 17 quantitative trait loci (QTLs) relative to 334 deletion breakpoints. The gene-containing fraction is 29% of the wheat genome present as 18 major and 30 minor gene-rich regions (GRRs). The GRRs varied both in gene number and density. The five largest GRRs physically spanning, 3% of the genome contained 26% of the wheat genes. Approximate size of the GRRs ranged from 3 to 71 Mb. Recombination mainly occurred in the GRRs. Various GRRs varied as much as 128-fold for gene density and 140-fold for recombination rates (Erayman et al., 2004).

Wheat genome cooperation with other species

Grasses are the single most important plant family in agriculture. Species from the grass family Poaceae provide an excellent model for Comparative analysis of genomes, as extensive genetic colinearity among several grass species has been described despite very heterogenous genome sizes and evolutionary divergence times of over 60 million years (Keller and Feuillet, 2000).

Comparison between wheat and rice genome

The wheat group 3 chromosomes shared the highest homology with rice chromosome 1 (Van Deynze et al., 1995). Analysis of the blastN results from the mapped group 3 unigenes against the rice genome indicated that the group 3 chromosomes share the highest level of homoeology with rice chromosome 1. Of the 537 ESTs used in the consensus map, 232 belonged to unigenes that shared significant similarity with portions of rice chromosome 1, 81 matched a rice sequence on another chromosome, and the remaining 215 ESTs did not significantly match any rice genome sequence to date. It was found that 59% of group 3 mapped-EST unigenes showed homology to rice (Munkvold and Showers, 1997). Sorrells et al. (2003) compared 4485 expressed sequence tags (ESTs) that were physically mapped in wheat chromosome bins, to the public rice genome sequence data from 2251 ordered BAC/PAC clones using BLAST. The increased resolution afforded by sequence analysis of 4485 mapped wheat unigenes revealed numerous discontinuities in gene order between wheat and rice that will complicate any transfer of information and markers between these species. Resolution of sequence similarity among species, genomes, and paralogs is variable among different genes due to evolutionary pressures as well as their respective physical genome location (Sorrells et al., 2003).

Comparison between wheat and barley

Except for ploidy differences, the wheat and the barley genomes are very similar in gene synteny and composition. A 1.1 Mb sequence for selected wheat and barley (*Hordeum vulgare* L.) regions showed that gene density within the GRRs may range from a gene every 4–103 kb with an average of 10–20 kb (Erayman et al., 2004; Patnaik and Khurana, 2001). The size of the 'gene-empty' blocks interspersed in these regions ranged from 0.8 to 94 kb. The region of high gene density was 40 kb long and contained 10 genes (a gene every 4 kb). The second largest contig among wheat and barley regions is 261 kb around the Mla locus (Erayman et al., 2004). A 130 kb region in the contig contained 23 genes with an average gene density of a gene per 5.6 kb. Size of the interspersing 'gene-empty' regions ranged from a few hundred base pairs to 11 kb. The largest 'gene-empty' region was 5.5 kb. Another 60 kb barley contig spanned a 32 kb region around the bronze locus with a gene every 3.2 kb (Erayman et al., 2004). Another study related to diploid wheat *T. monococcum* and barley conducted by Dubcovsky et al. (1996). In this study it was found that linkage groups of both grasses are remarkably conserved. They differ by a reciprocal translocation involving the long arms of chromosomes 4 and 5, and paracentric inversions in the long arm of chromosomes 1 and 4; the latter is in a segment of chromosome arm 4L translocated to 5L in *T. monococcum*. Devos et al. (1994) revealed a high degree of colinearity between maize chromosome 9 and the group 4 and 7 chromosomes of wheat genetic maps. The order of DNA markers on the short arm and a proximal region of the long arm of the genetic map of maize chromosome 9 are highly conserved with the marker order on the short arm and proximal region of the long arm of the genetic maps of the wheat homeologous group 7 chromosomes. A major part of the long arm of the genetic map of maize chromosome 9 is homeologous with a short segment in the proximal region of the long arm of the genetic map of the wheat group 4 chromosomes. Evidence is also presented that maize chromosome 9 has diverged from the wheat group 7 chromosomes by both a pericentric and a paracentric inversion. The paracentric inversion is probably unique to maize among the major cereal genomes (Devos et al., 1994).

Phylogenic relationship between wheat, rice and maize

Extra chromosomal inheritance is most reliable tool to find out phylogenic relationship between species. Among this Chloroplast genes have been used extensively to reconstruct the phylogeny in the Poaceae. Matsuoka et al. (2002) constructed a chloroplast genome type for each species by extracting and concatenating the variable sites from the aligned gene sequences of maize, rice, wheat, and tobacco. Of the 106 genes, 98 had more than one variable site. They used three gene groups for analysis: (1) all 98 genes; (2) 94 genes, excluding four genes *(ndhB, psbD, psbH, andrrn23*) that showed highly significant rate heterogeneity of nucleotide substitution ($P < 0.001$) in relative rate tests on the entire sequences; and (3) 84 genes, excluding all 14 genes that showed significant rate heterogeneity ($P < 0.05$). The total number of variable sites and average number of variable sites per gene, respectively, ranged from 8324 to 9675 bp and from 98.7 to 99.1 bp. Saitou and Nei (1987) were constructed Variable site–based phylogenetic trees of these three cereal chloroplast genomes by means of the neighbor-joining algorithm. All three trees have the same topology (Fig.1), which supports a close relationship between the rice and wheat chloroplast genomes (52-87% for bootstrap, 88-99% for the interior test). This suggests that rice and wheat had a common ancestor, which was not involved in the lineage leading to modern maize. The highest statistical supports for the rice-wheat clade (87% for bootstrap, 99% for the interior test) were obtained when the four genes (*ndhB, psbD, psbH* and *rrn23*) that showed highly significant rate heterogeneity of nucleotide substitution ($P <0.001$) in the relative rate tests were excluded (Matsuoka et al., 2002).

Table 1. Examples of improved stress tolerance wheat varieties generated through biolistic transformation.

Improved variety	Selectable/scorable markers used	References
Fungal resistance	*bar*	Chen et al. (1998)
Herbicide resistance	*Pmi* and *bar*	Gadelata et al. (2006)
Fertile variety	*Basta* (Glufosinate-ammonium)	Becker et al. (2002)
Herbicide resistance	*CP4* and *GOX* genes	Zhou et al. (1995)
Increased draught strength and stability	*bar* and *uidA*	He et al. (1999)
Pest resistance	*Cah* encoding enzyme cyanamide hydratase	Weeks et al. (1998)
Fertile wheat	*hpt*	Ortiz et al. (1996)
Drought resistant wheat	*DREB1A* and *bar* genes b	Pellegrineschi et al. (2004)
Insect resistance	Trypsin inhibitor activity assay	Altpeter et al. (1999)
Drought resistance	*bar* and *gus*	Patnaik and Khurana (2003)
Drought and salt tolerance	Selectable marker	Shiqing et al. (2005)

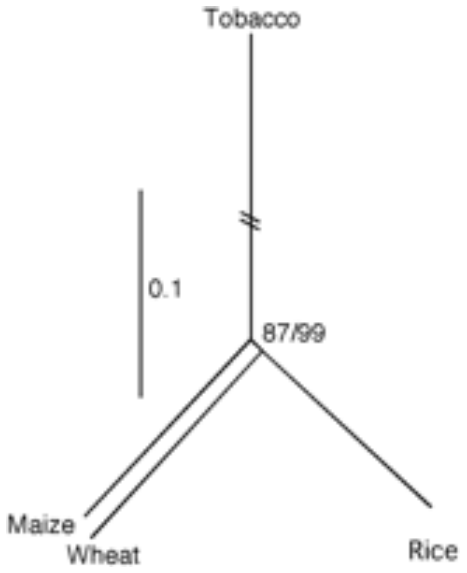

Fig 1. Phylogeny between three major cereal crops. Source: Matsuoka et al. (2002)**.** Published with kind permission from the journal of Molecular Biology and Evolution, Oxford University Press, 2011.MBE. 2002. 19: 2084 2091.

Transgenic wheat

The introduction of foreign genes encoding for useful agronomic traits into commercial cultivars has resulted in saving precious time required for introgression of the desired trait from the wild relatives by conventional practices and alleviating the degradation of the environment due to the use of hazardous biocides (Patnaik and Khurana, 2003). All plants (including wheat) can be changed genetically by using two basic approaches: 1) transformation, and 2) the use of known DNA markers. Transformation involves the introduction of genes into a plant from some outside foreign source, like a fungal pathogen. The pathogen can carry the trait into the parent plant (Ahmad and Shaikh, 2003; Jones, 2005). The use of DNA markers, on the other hand, allows a gene to be inserted into a plant using what is already known about the chromosomes of a plant through the mapping process. It also allows the "pyramiding" of one trait or another. At present, the process of transformation in wheat has been carried out most successfully in spring wheat, notably the Bob White variety. Any engineered spring wheat would have to be back-crossed into winter wheat (Lochmiller et al., 1993). Transformation of wheat is actually carried out either by a so-called gene gun or by the use of a bacterial vector (*Agrobacterium*) in a dish in a laboratory. Wheat researchers agree that there appears to be a tremendous potential for wheat improvement, as biotechnology could be used to add. In recent years, wheat improvement efforts have therefore focused on raising the yield potential, quality characteristics, resistance to biotic stresses (herbicide resistance, disease resistance, including viral disease resistance etc.) and tolerance to abiotic stresses (*eg*. drought

Table 2. Genetic transformation of wheat for pathogen and pest resistance Source: Patnaik and Khurana (2001). Published with kind permission from Electronic Journal of Biotechnology Feb 22, 2011. EJB ISSN: 0717-Vol.4 No. 2, Issue of August 15, 2001. pg. 101, table no .4.

Gene	Source	Mode of Action	Construct (Promoter)	Comment/Reference
Coat Protein	Barley yellow mosaic virus	Coat protein-mediated resistance	pEmuPAT-cp (35S)	Karunaratne et al. (1996)
Ribosome Inactivating protein (RIP)	*Hordeum vulgare* L.	Specific glycosidases that remove a conserved adenine residue from the large rRNA of the large ribosomal subunit Inactivates ribosome and blocks translation elongation	pRipChi (Ubi) *I-Sec1* (35S-RTBV intron)	Interfere with normal plant regeneration and development, Bliffeld et al. (1999) Moderate/no protection against *Erysiphe graminis*, Bieri et al. (2000)
Chitinase	*Oryza sativa* L.	Cell wall degradative enzyme Act on cell wall polysachharide, chitin	pAHG11 Chi11_Ubi pro-bar-nos	Lack of transgene expression, Chen et al. (1999)
	Hordeum vulgare L.		Ubi	Increased resistance to infection by *Erysiphe graminis*, Bliffeld et al. (1999)
Thaumatin like Protein (*tlp*)	*Oryza sativa* L.	Alter membrane permeability and/or Cellular signal transduction cascades	pGL2ubi-tlp (Ubi/tlp/CaMV 35S/hpt)	Enhanced resistance against *Fusarium graminnearum* in T_1, T_2 and T_3 plants, Chen et al. (1999)
Stilbene synthase	*Vitis vinifera* L.	Phytoalexin synthesis Synthesizes the phytoalexin trans-reveratrol	pGBI, pGBII (Vst1)	Induction of stilbene synthase mRNA after wounding and infection in T_1 and T_2 plants, Leckband and Lorz, (1998)
Killer protein (KP)	*Ustilago maydis* infecting virus	Virally encoded antifungal protein. Inhibit growth of sensitive cells	pUbi:KP4 (Ubi)	Increased endogenous resistance against *Tilletia tritici*, Clausen et al. (2000)
Lectin	*Galanthus nivalis* agglutinin	Binding to the insect gut surface	pRSsGNA (*Rss1*) pUbiGNA (Ubi)	Decreases the fecundity, but not the survival of the grain aphid *Sitobion avenae*, Stoger et al. (1999)
Proteinase Inhibitor	*Hordeum vulgare* L. (barley trypsin inhibitor-CMe)	Regulators of endogenous proteinases Lower protease activity in insect guts leading to direct shortage of amino acids	C-Me (BTI-CMe) pUPMBI-66 (Ubi)	Inhibition of early insect larvae in transgenic seeds; No significant effect on leaf feeding insects, Altpeter et al. (1999)

tolerance) and depending on the regional requirement of the crop. Genetic engineering provides an alternative approach to enhance the level of resistance (Mackintosh et al., 2007). Table 1 describes the examples of stress tolerant wheat varieties.

Biotic stress resistance wheat

Most of the works on genetic engineering of wheat for resistance against biotic stress have focused on developing protection against fungal pathogens (Ray et al., 2003). Fusarium Head Blight (FHB), or scab, is a fungal disease caused by *Fusarium graminearum* and other *Fusarium* species, affecting many small grains cereals, but is of most importance on wheat. FHB reduces kernel weight and consequently grain yield. The germination rate and seedling vigour are reduced when the seeds are infected. The fungus digests proteins and starch and the use of infected kernels generates technical problems because enzymes and yeast growth are inhibited by by-products of the fungus that

prevent bread production (Mardi et al., 2005). It is determined that *F. graminearum* secretes many extracellular enzymes (Jenczmionka and Schäfer, 2005; Paper et al., 2007) which are postulated to play a role in fungal infection. One characteristic of the wheat response to *F. graminearum* infection is the induction of defense response genes such as *β-1,3-glucanase*, *tlp-1*, and thionin genes (Zhou et al., 1995). These genes are thought to provide basal resistance during infection because they encode proteins with differing modes of action against fungal pathogens. Thionins and tlps damage fungal cell membranes by making them permeable (Bohlmann et al., 1988), whereas β-1,3-glucanases degrade cell wall polysaccharide linkages (Leah et al. 1991). Mackintosh et al. (2007) produced transgenic wheat lines overexpressing either *α-1-purothionin*, a *tlp-1*, or a *β-1,3-glucanase* to test their efficacy against FHB. Following table 2 shows details of transgenic wheat resistance against different pests and pathogens, genes encoding for viral coat proteins, antifungal proteins, and proteinase inhibitors that have been successfully introduced.

Abiotic stress resistance wheat

A number of abnormal environment parameters such as drought, salinity, cold, freezing, high temperature, anoxia, high light intensity and nutrient imbalances etc. are collectively termed as abiotic stresses. In addition, more than one abiotic stress can occur at one time. For example, high temperature and high photon irradiance often accompany low water supply, which can in turn be exacerbated by subsoil mineral toxicities that constrain root growth. Furthermore, one abiotic stress can decrease a plant's ability to resist a second stress (Tester and Bacic, 2005). In many species, salt sensitivity is associated with the accumulation of sodium (Na^+) in photosynthetic tissues. Na^+ uptake to leaves involves a series of transport steps and so far very few candidate genes have been implicated in the control of these processes. Drought is a major abiotic factor that limits crop productivity, thereby causing enormous loss. Davenport et al. (2005) was compared Na^+ transport in two varieties of durum wheat (*T. turgidum*) L. subsp. *durum* known to differ in salt tolerance and Na^+ accumulation; the relatively salt tolerant landrace line 149 and the salt sensitive cultivar Tamaroi. The major differences in Na^+ transport between the genotypes were (1) the rate of transfer from the root to the shoot (xylem loading), which was much lower in the salt tolerant genotype, and (2) the capacity of the leaf sheath to extract and sequester Na^+ as it entered the leaf. The genes encoding the late embryogenesis proteins (*LEA*) which accumulate during seed desiccation, and in vegetative tissues when plants experience water deficiencies have recently emerged as attractive candidates for engineering of drought tolerance (Patnaik and Khurana, 2003). Transgenic approach has been used for successfully introducing and overexpressing the barley *HVA1* gene encoding for a late embryogenesis abundant (*LEA*) protein by Sivamani et al. (2000) into wheat by particle bombardment. Plants with a winter growth habit flower earlier when exposed for several weeks to cold temperatures, a process called vernalization. Yan et al. (2004) reported the positional cloning of the wheat vernalization gene *VRN2*, a dominant repressor of flowering that is down-regulated by vernalization. Loss of function of VRN2, whether by natural mutations or deletions, resulted in spring lines, which do not require vernalization to flower. Reduction of the RNA level of *VRN2* by RNA interference accelerated the flowering time of transgenic winter-wheat plants by more than a month (Yan et al., 2004). The production of transgenic crop plants is an expanding component of agricultural biotechnology. For commercial success, it will be crucial that the introduced traits be transmitted faithfully through successive generations in a predictable manner. Zainuddin (2005) demonstrated that transgenes integrated into transgenic wheat obtained via microprojectile bombardment method could be transmitted and, in most cases, expressed until the third generation. The expression of the *GUS* gene was stable as observed in leaves, microspores, anthers, ovaries and seeds. Nevertheless, the bar gene appeared to undergo a reduction or disappearance in expression in a number of plants from the first to the third generation (Zainuddin, 2005). Srivastava et al. (1999) used strategy based on site-specific recombination to ensure transfer of only a single copy of a foreign gene in the plant genome of wheat. To achieve this they transform vector consists of a transgene flanked by recombination sites in an inverted orientation. Regardless of the number of copies integrated between the outermost transgenes, recombination between the outermost sites resolves the integrated molecules into a single copy. As the experiments related to transgenics increases some problems are also crop up but for the sake of food crises scientists are continue try to find out the way. Application of biotechnology will thus contribute greatly to improving yield stability by generating plants with improved resistance to biotic and abiotic stresses rather than raising the overall yield. The coming years will undoubtedly witness an increasing application of biotechnology for the genetic improvement of wheat (Patnaik and Khurana, 2001).

Conclusions and future directions

Study of cereal crops has been a most popular research field with lots of possibilities. Development of biotechnology tools has opened a new avenue for genetic advancement of wheat crop. Genetic complexity of wheat is a major obstacle in crop improvement but phylogenic study and genetic engineering make it possible to see the evolutionary relationship between major cereal crops as well as to find out genes related to stress stimulus. Wheat genome shows similarity with chromosome 1 of rice and chromosome 9 of barley. Among these homologous regions some non homologous genes are also exist which are conserved and phylogenic important are necessary to be identified for more accurate results. Study of similarity of genomic configuration among closely related species are also important for development of transgenic plant as well as to develop new cultivation strategy, in wheat most of the transgenic verities are developed through insertion of rice genes. In development of transgenic tools study of selectable markers are of great importance. In most of cases bar and gus gene is used but because of it's microbial origin many factors have to be considered before using. So there is need to find out more sensitive and easily available markers for selection. Although gene-transformation techniques combat the challenges related to abiotic and biotic stress for cultivars but there are many snags have to overcome to make biotechnological tools more apparent, real buy and cherry pie.

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